Natural selection and sociobiology

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Plotkin & Odling-Smee (P&O) set themselves the task of reconciling the "older sciences" with sociobiology. They criticise the "monolithic theory" that natural selection has been responsible for evolution and advise sociobiologists to discard this view in favour of their multiple-level theory. This, they hope, will make sociobiology more acceptable.

To counter this view in favour of their multiple-level theory, P&O criticise is the theory of natural selection as stated by Fisher (1930; 1958), though they attribute it to others. P&O say that the gene "is well able to supply adaptations or those aspects of the world which are relatively permanent..." A gene can do no such thing. The most it can do is provide a small selective advantage to its bearer in a particular environment. This advantage ensures that, after a large number of generations, the organism will be well adapted to that particular environment. P&O go on to say that the gene cannot provide adaptations for those events which "last long enough to have an impact on the animal and that must be adapted to, yet may change and change again..." P&O fail to appreciate that the adaptation made by natural selection is the totality of the environment which must, by definition, include the type of environment they mention. It is this failure which leads them to develop their model of multiple-level of evolution.

P&O's grasp of the meaning of "adaptation" is uncertain. Fisher (1930; 1958) explains it beautifully. Adaptation is a relative term. An organism is well adapted to its environment only insofar as investigators can envisage another environment to which it is less adapted. Thus, adaptation can be discussed statistically. If O represents the complex environment of an organism and A its position, then any point within the hypersphere with its centre at O and passing through A represents a better adaptation. A point outside this hypersphere represents a worse adaptation. The respective positions of O and A can be interchanged. A change in environment which is represented by a point outside the hypersphere with its centre at A and passing through O, may require readaptation to the environment only if it is sufficiently removed from the hypersphere, assuming that the organism is well-adapted to environment. Minor changes in environment may need no adjustment. The flaw in the theory of evolution by natural selection, which P&O detect and which they seek to remedy by their multiple-level theory, is imagined rather than real.

I find P&O's conception of natural selection amusing. They say... "...even though cultural adaptive traits can be transmitted nongenetically, they still cannot escape ultimate evaluation by natural selection." Again, "...natural selection is indifferent to the source of any adaptation," etc. It needs to be stated clearly that natural selection means nothing more than the differential reproduction by different genotypes and that it affects only those traits which are transmitted genetically. It cannot "evaluate" a nongenetic trait. P&O also appear to have been unable to distinguish sufficiently between cultural and genetic adaptation. My criticism of their position can best be explained by means of an example. Consider two males, A and B, both born at the turn of the century and now past their reproductive period. A was a professor at a well known university. His contributions to science are well known. His is, in fact, a household name. He felt he could not afford the time to marry and rear children. B has been out of prison as often as he has been in it. However, he found sufficient time to marry and his wife has reared ten children with some help from the state. Which of the two is better adapted? The answer depends on whether your interest lies in cultural or genetic adaptation. Genetically, B is better adapted, for it is his progeny who will inherit the earth. In this case, natural selection has evaluated the cultural adaptation by eliminating it. However, I suspect this is not the sort of evaluation P&O have in mind.

What is sociobiology? I will use a famous analogy; it is the assertion that in an elephant a gene has found a way of making a gene. Why should the gene make such a complex "survival machine"? Presumably because this is the only way it can survive. Yet many more survival machines (i.e., species) are extinct than exist today. Maybe these survival machines provide a survival outfit for some genes. Such a restatement may also help to explain the conflict between species as well as tribal wars, but it is unlikely to be acceptable to most sociobiologists.

In primitive times, there was, perhaps, only one gene. All other genes are derived from it by mutations. It is far from certain that a simple duplication would have been less efficient in spreading it than the invention of survival machines. I find it surprising that this powerful entity which, we are told, directed evolution towards survival machines has found no way to ward off deleterious mutations which destroy survival machines indiscriminately. Consider sex: it was, presumably, evolved by the gene to produce bigger and better survival machines. Yet this is also the mechanism which eliminates many genes. Perhaps the gene is practicing eugenics by eliminating bad genes!

What is the fate of an individual gene in a population? Fisher (1930; 1958) showed that it must become extinct sooner or later if it has no selective advantage. With some selective advantage it may become fixed in a population, but this does not insulate immortality because species also become extinct. The future of a single gene is hopeless indeed. I cannot see how, in the face of this certainty, one can construct a scientific hypothesis which assumes a gene's immortality.

Natural selection is never irrelevant. If a species is not well-adapted to its environment, selection helps it to adapt better. For a well-adapted species, selection helps to maintain that adaptation. These two roles of natural selection differ. The former, but not the latter, has evolutionary consequences. However, natural selection has no relevance to a trait which is not genetically determined. I find many claims of sociobiology to be unacceptable and will remain sceptical until sociobiologists show, conclusively, that a complex behavioral trait is genetically determined. P&O's attempt to make it more acceptable indicates to me how good intentions, when based on half-understood concepts, lead one astray.

Indeterminacy is inherent in an inadequate model of evolution, not in nature

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Plotkin & Odling-Smee's (P&O's) critique of a "monolithic theory" of evolution espoused by prominent sociobiologists...
Commentary/Plotkin & Odling-Smee: Multiple-level evolution and sociobiology
draws attention to the roles of learning, culture, and society in
evolution. Insofar as it opposes the simple-minded genetic
determinism so prevalent in this field, it shows a positive
trend of thought, although it is somewhat surprising that the
authors do not make reference to previous discussions of
cultural transmission by Cavalli-Sforza and Feldman (1978)
or by Rao et al. (1976). However, P&O's paper has several
shortcomings which make the alternative model they propose
undeniable.

**Determinism and natural law.** P&O advocate that the
future course of evolution is "fundamentally unpredictable"
because of the indeterminacy and randomness supposedly
inherent in complex interactions within and between 'levels' of
their model. They state boldly that "evolution is not a
deterministic process."

It is instructive to refer to the opening sentence of the fifth
chapter of Darwin's *Origin of Species* where he states: "I
have hitherto sometimes spoken as if the variations—so
common and multifid with organic beings under domestica-
tion, and in a lesser degree with those under nature—were
due to chance. This, of course, is a wholly incorrect expres-
sion, but it serves to acknowledge plainly our ignorance of the
cause of each particular variation."

The problem with a proclamation of randomness and
unpredictability is that it may merely reify the theoretist's own
lack of knowledge and understanding, thereby discouraging
further efforts to investigate and analyse phenomena. P&O
are quite right in their opinion that living systems entail a
plethora of exceedingly complex interactions that can never
be understood by simplistic sociobiology, but I think they are
wrong in their despair about prospects of understanding this
web of interactions.

Furthermore, the present difficulty of predicting the
future should not be made to weigh so heavily on only one
aspect of the problem— the evolution of organic species. We
cannot even predict what the inorganic environment will be
like millennia from now, although the properties of this envi-
noment, of course, depend to some extent on developments
in the realm of life. At any rate, without an accurate estima-
tion of the conditions of life, it is impossible to predict the
responses of living beings to changed conditions.

The complexity of the system shows the need for a great
deal more investigation of nature and of real interactions
before we retire to the armchair and pass judgment on nature,

**Adaptation and natural selection.** P&O assert that natural
selection is "one of nature's universals," which evaluates
"culturally derived adaptations in the same way as any other
adaptation"; this implies that selection is the basis for all
evolutionary progress.

There is no doubt that there can be competitive struggle
between cultures that may even lead to the extinction of
certain features of a culture. However, adaptation or innova-
tion and cultural transmission can also take place without
selection. Because of the rapidity of cultural transmission
throughout a population within an individual's lifetime, and
because cultural innovations come into being as solutions for
widespread problems (e.g. disease) in nonrandom ways, it is
possible for a new adaptation to be universally adopted in
short order. This does not free a species from the reality of
natural selection, but it does show that adaptation and selec-
tion are two separate and distinct sources of evolutionary
change. Through cultural adaptation and transmission,
progress is possible without the need for part of the popula-
tion to fail. The conditions of living for the whole of society
can be elevated.

**The fundamental tautology.** When P&O tell us that "one
can never escape from natural selection," they seem to be
using selection in its tautological sense: the most fit will
propagate best; those that propagate best shall be called the
most fit. Darwin rose above this mundane level by propos-
ing that natural selection, which was obvious to almost everyone
was in fact a creative force, which could lead to the develop-
ment of a new species—something qualitatively different
from its ancestors.

P&O do not inform us about the fundamental problem of
evolution: speciation. In some places they try to account for
why a species is well-adapted to the conditions of life here
and now, and why certain historical changes may occur
within a species. But on a central problem of evolutionary
theory today, the gradual or abrupt transition to a new
species, their model is silent.

P&O's speculations about genetic determination of learn-
ing ability and the "capacity for culture" are topics of current
debate relating to attributes of human races and social classes
and in the present target article these are topics presented in
simple terms that could easily be misunderstood or misused.

**The gene-learning dichotomy.** Like so many others in this
field (e.g. Lorenz) P&O adhere to the dogma that there are
only two means of information acquisition and transmission—
genes and learning. This reveals a rather narrow perspective
on heredity. Consider just three of the many other mecha-
nisms: Cytoplasmic inheritance (Grum 1976) involves trans-
mission of non-nucleic organelles and structural details such as
mitochondria, endoplasmic reticulum, Golgi apparatus, cell
membrane, etc. Certain of these contain their own DNA but
many do not. The key thing here is that cytoplasmic struc-
tures are not organized *de novo* by gene products acting on a
disorganized pool of central intermediates. On the contrary,
new structures are built using existing structures as templa-
tes (Lehninger 1967). The fertilized egg contains a diverse array
of structures in a well-organized cytoplasm, and these
nongenetic components of heredity are reproduced and trans-
mitted from old cells to new.

The position of a structure in the cell can be transmitted to
new cells. This is clearly evident in protozoa, where microsur-
urgical modifications of the cilia in the cell surface are perpetu-
ated for many generations. The importance of such "posi-
tional information" is now being recognized in multicellular
organisms as well (see Subtelny & Konigsberg 1979). (See also
Corballis & Morgan: "The Biological Basis of Human Lateral-
ality" BBS 2(2) 1978.)

In mammals, inheritance may also entail transmission of
viruses, antibodies and various chemicals directly from mother
to offspring via placental transfer or the milk; even transmis-
sion of an acquired immunity via the father has been claimed
(Steele 1979).

Thus P&O's assertion that animals "cannot transmit any of
their nongenetic adaptations nongenetically" is simply not
valid. This omission is especially serious because nongenetic
mechanisms of inheritance appear to be more plastic than
chromosomal DNA-based mechanisms; they are downright
Lamarckian in some instances.

**Culture in a nutshell.** P&O argue the interesting point that
natural selection makes no distinction "between a cultural
and a nongenetic adaptation within the same animal"; this is
similar to saying that selection acts on phenotypes, not geno-
types. This notion raises a very big question about the
meaning of culture. The authors consider culture to be
founded upon associative learning ability, but this scheme
leaves out a host of nongenetic, nonlearning aspects of life
that appear to function almost the same way that culture,
narrowly defined, does.

Consider an oak tree laden with acorns. The fact that the
tree has reached reproductive maturity proves that its envi-
noment nurtures that particular species of oak. By dropping
its acorns onto fertile ground, the parent transmits one aspect
of its environment to its offspring. And what about the
nutrient-rich endosperm and the seed coat of the nut itself?
They are separate from the embryo proper, yet they are
transmitted from parent to offspring.

Between nuclear genes and associative learning there is a vast profusion of phenomena in plants and animals alike, and any theory, such as the one diagrammed in P&O's Figure 2, which totally neglects this is not a valid reflection of nature but is, rather, a product of imagination inspired by narrowly circumscribed facts about nature. Having left so much out of their analysis, it is no wonder that P&O cannot even begin to make accurate predictions about the future course of evolution.

**A defense of monolithic sociobiology and genetic mysticism**

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Plotkin & Odling-Smee (P&O) give a nicely reasoned account of the way natural selection, by adjusting gene frequencies when it acts on phenotypes, has its lasting effects. Selection is always between organisms, never within, and it is always on phenotypes transcribed from genotypes, with no possibility of communication from phenotype to gene. However complex the events on P&O's levels 2 and 3 might be, these levels have evolutionary significance only to the extent that they affect the gene-frequency arrays of level 1. I am a bit surprised at the implication that sociobiologists, radical or otherwise, should see anything controversial in recognizing that evolution can provide organisms "... with some capacity for autonomous information gain and storage." Organs that collect and use information are not less biological than those that collect and use food. I suspect that the distinction between levels 2 and 3 is a bit arbitrary, and that more levels might be recognized, but this would not affect their reasoning, or the validity of the monolithic theory for phenotypic features at these levels.

There is nothing arbitrary about level 4. P&O show convincingly that there is a novel process here and that level 4 requires some special attention not needed at lower levels. The novel process is cultural inheritance, which may be considered Larmorckian only in the special sense that inherited features are not coded in the genes, rather than in the usual sense that phenotypic features are being transcribed onto the germ plasm. I can find no fault with the statement of conditions necessary for cultural inheritance. Also, I accept most of their comparisons between level-1 and level-4 modes of inheritance, but I believe that P&O are led astray by a failure to appreciate some of the similarities.

Cultural traits, memes as Dawkins's (1976) cited book terms them, are subject to natural selection - not because they affect the fitness of organisms - but because they are replicators (like genes) and have a mechanism of inheritance. The natural selection of memes is subject to the same rules and limitations as the natural selection of genes. A gene may be favorably selected without having developmental effects (by segregation, distortion, and other processes) or in spite of what might be considered unfortunate effects. Sexual competition, for example, may select for genes that reduce both individual viability and efficiency of resource utilization by the group. Likewise, cultural traits may be favorably selected despite unfortunate consequences for biological fitness, such as learning capacities, are developed characters that have ultimate evolutionary explanations. P&O are right that the monolithic theory is of little help in establishing links among genes, development, learning and socioculture. Their quotation from Rosenblatt (1976) is also valid; we need a convincing way of relating these different levels of behavioral organization, and this need is not met by sociobiology. My guess is that their multilevel theory is a bit too abstract a level to constitute an effective beginning for a theory of behavioral ontogeny. If and when we get a detailed scientific picture of the development of social behavior in human and other cultural animals, I would expect sociobiology to have a role in explaining phylogenetic variation in the details of that picture.

**Authors' Response**

**Possible mechanisms for a multiple-level model of evolution**

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Many of the commentaries cohere around two major points of criticism. The first is that we have omitted discussion of the mechanisms that are assumed to operate at levels 2, 3, and 4. Campbell, Cloak, Dew-